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Denitrification and DNRA in Urban Accidental Wetlands in Phoenix, Arizona

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Key Points:

- Dissimilatory nitrate reduction to ammonium (DNRA) accounted for up to 40% of nitrate reduction (DNRA plus denitrification) in the urban accidental wetlands in Phoenix, Arizona, USA
- DNRA rates differed among wetland patches with unique plant species and these differences were not driven by dissolved organic carbon
- Perennial accidental wetlands have a high capacity to attenuate nitrate loading through both DNRA and denitrification

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract

Denitrification and dissimilatory nitrate reduction to ammonium (DNRA) both require low oxygen and high organic carbon conditions common in wetland ecosystems. Denitrification permanently removes nitrogen from the ecosystem as a gas while DNRA recycles nitrogen within the ecosystem via production of ammonium. The relative prevalence of denitrification versus DNRA has implications for the fate of nitrate in ecosystems. Unplanned and unmanaged urban accidental wetlands in the Salt River channel near downtown Phoenix, Arizona, USA receive high nitrate relative to non-urban wetlands and have a high capacity for denitrification, but unknown capacity for DNRA. We conducted in-situ push-pull tests with isotopically labeled nitrate to measure denitrification and DNRA rates in three of the dominant vegetative patch types in these urban accidental wetlands. DNRA accounted for between 2% and 40% of nitrate reduction (DNRA plus denitrification) with the highest rates measured in patches of *Ludwigia peploides* compared to *Typha spp*. and non-vegetated patches. The wetland patches were similar with respect to dissolved organic carbon concentration but may have differed in carbon lability or strength of reducing conditions due to a combination of litter decomposition and oxygen supply via diffusion and aerenchyma. The ratio of DNRA to denitrification was negatively correlated with nitrate concentration, indicating that DNRA may become a more important pathway for nitrate attenuation at low nitrate concentration. Although DNRA was generally lower than denitrification, this pathway was an important component of nitrate attenuation within certain patches in these unmanaged urban accidental wetlands.

Plain Language Summary

Urban waterways commonly have higher nitrogen concentrations relative to non-urban systems, which can damage ecosystems. Wetlands support microbes that can carry out denitrification, which removes a deleterious form of nitrogen, and dissimilatory nitrate reduction to ammonium (DNRA), transforming to a less mobile but still potentially deleterious form of nitrogen, thus recycling the nitrogen in the system. We measured these two transformations in urban accidental wetlands in Phoenix, Arizona, USA. We found DNRA was ubiquitous and could account for as much as 40% of the combined rates. Both denitrification and DNRA were higher in places covered by certain plant species than in other wetland areas. These plants may create conditions more favorable for microbes because the plant produces substances that are easily consumed by the microbes or because they regulate oxygen conditions through roots. Overall, we found that DNRA was a small yet substantial pathway for nitrogen recycling in these urban wetland ecosystems.

1. Introduction

Nitrogen is an essential, often limiting, element for biological growth that can act as a pollutant if present at high concentrations. Excessive nitrogen in highly biologically available forms, especially nitrate (NO_3^-), is common in urban ecosystems. Urban ecosystems tend to have higher NO_3^- burdens due to higher inputs from fertilizer application (Baker et al., 2001; Law et al., 2004), deposition from fossil fuel combustion (Bettez & Groffman, 2013; Hale et al., 2014), and treatment of sewage (Lauver & Baker, 2000). In addition, urban stormwater infrastructure quickly transports runoff to storm drains that can discharge into water bodies (Baker et al., 2001; Kaye et al., 2006). Whether this high NO_3^- burden causes eutrophication partially depends on the capacity of the aquatic ecosystem to attenuate NO_3^- inputs. Wetland ecosystems can be hotpots for NO_3^- attenuation due to the availability of water, organic matter, and variable oxygen zones (Ehrenfeld, 2000; Mitsch & Gosselink, 2015). These environmental conditions are conducive to NO_3^- attenuation through pathways such as denitrification and dissimilatory NO_3^- reduction to ammonium (NH_4^+) (DNRA). Indeed, urban wetland ecosystems are thought to play an outsized role in urban ecological infrastructure that reduces urban NO_3^- loads (Harrison et al., 2011; Palta et al., 2014).

Urban accidental wetlands form in low lying locations where water and organic matter can accumulate (Palta et al., 2017). These ecosystems are defined by their formation without planning or design, but instead "accidentally" as the result of municipal decisions and infrastructure designed for other purposes, such as stormwater management (Palta et al., 2017). In desert cities, where both water and resources are scarce, accidental urban wetlands represent an important component of urban ecological infrastructure. For example, urban accidental wetlands in Phoenix, Arizona, USA, have developed in the historically dry Salt River channel, with the proliferation of hydric soils and wetland vegetation in some locations (Banville & Bateman, 2012; Bateman et al., 2015; Suchy et al., 2019). These ecosystems have only recently become a focus of investigation, with research demonstrating that urban accidental wetlands can provide habitat for wetland vegetation and wildlife (Banville & Bateman, 2012; Bateman et al., 2015; White & Stromberg, 2011), promote NO_3^- and phosphorus removal from surface water (Palta et al., 2017), and support high potential denitrification rates (Suchy et al., 2019). To date, however, only a limited number of studies have investigated DNRA in urban wetlands across the globe (Jahangir et al., 2017; Rahman, Grace, et al., 2019; Rahman, Roberts, Grace, et al., 2019; Rahman, Roberts, Warry, et al., 2019; Scott et al., 2008) and there have not been any reported DNRA measurements in urban accidental wetlands.

Denitrification is an important and well-studied pathway of NO_3^- attenuation because the process converts NO_3^- to nitrogenous gases that are emitted from the system, thus reducing the overall nitrogen burden (Boyer et al., 2006; Groffman et al., 2004; Kaushal et al., 2008). DNRA, while requiring conditions similar to denitrification, effectively recycles nitrogen within the ecosystem by converting biologically available NO_3^- to biologically available NH_4^+. The resulting NH_4^+ is available for plant uptake, assimilation by organisms, and nitrification, thereby conserving the element within the ecosystem (An & Gardner, 2002). Although less studied compared to denitrification, DNRA has been measured in many of the same ecosystems where denitrification is found, including coastal ecosystems (see Giblin et al., 2013 for a review), streams (Kelso et al., 1997; Storey et al., 2004), lakes (Brunet & Garcia-Gil, 1996), constructed freshwater wetlands (Scott et al., 2008), hot springs (Dodsworth et al., 2011), soils (Rütting et al., 2011; Silver et al., 2001), and urban ecosystems (Dunn et al., 2013; Jahangir et al., 2013; Rahman, Grace, et al., 2019; Rahman, Roberts, Warry, et al., 2019; Wei et al., 2020). Understanding the relative rate of denitrification and DNRA has consequences relating to the extent that nitrogen in NO_3^- is removed from or conserved in the ecosystem. Tiedje (1988) proposed that denitrification is favored under high NO_3^- and high organic carbon conditions, whereas DNRA is favored under low NO_3^- and high organic carbon conditions because the process transfers a higher number of electrons per mole of NO_3^-. Studies to date have had varied results with respect to this hypothesis (Crenshaw et al., 2010; Kelso et al., 1997; Matheson et al., 2002; Nizzoli et al., 2010; Rahman, Roberts, Grace, et al., 2019; Scott et al., 2008; Storey et al., 2004), with some suggesting the rates of DNRA relative to denitrification are driven by differences in organic carbon availability (Fazzolari et al., 1998; Matheson et al., 2002; Nijburg & Laanbroek, 1997). Our study seeks to inform and expand upon previous work by investigating the relative rates of denitrification and DNRA in different vegetation patches of urban accidental wetlands.

Plant cover and type are often drivers of nitrogen transformations including denitrification and DNRA. Vegetation can alter soil conditions by creating macropores for the exchange of gases, increasing soil aggregates, and providing a source of organic carbon via litter and root exudates (Alldred & Baines, 2016). The supply of organic compounds from litter and exudates provides an energetic base for heterotrophic consumption, thus lowering oxygen availability and promoting reducing conditions (Matheson et al., 2002). Plant litter quality, as measured by labile and structural carbon content, can directly affect carbon availability to microbial communities (Hume et al., 2002). Plants that have more structural carbon compounds, such as lignin, produce litter that is less bioavailable than plants with lower structural carbon content. Therefore, as the type and lability of carbon changes among different plant patch types, so too will the magnitude of NO_3^- reduction processes. The Salt River wetlands host many obligate wetland plants (Bateman et al., 2015), but two patch types of aquatic macrophytes dominate the cover in perennially inundated wetlands. The first patch type is comprised of *Ludwigia peploides* (floating primrose-willow) a floating aquatic macrophyte that forms a dense network of stems through the water column. The second patch type comprises two species of cattail: *Typha domingensis* (southern cattail) and *Typha latifolia* (broadleaf cattail). The floating species of *L. peploides* is expected to have less structural carbon compared to the *Typha spp* that can grow up to several meters above the water surface. These plant species occupy

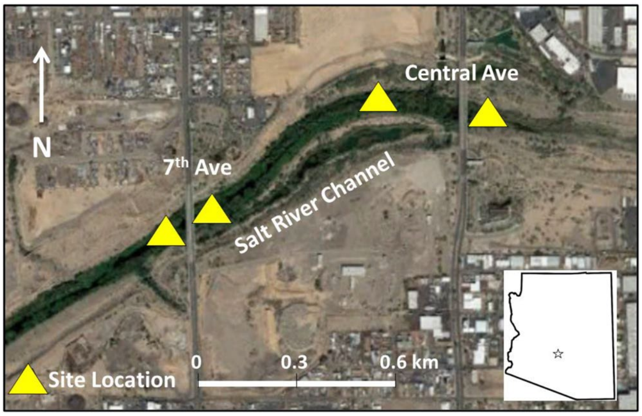

Figure 1. Map of field sites in the Salt River channel near downtown Phoenix (Arizona, USA). The push-pull experiment was conducted at two sites, 7th Avenue and Central Avenue, and at two sampling locations within each site, west (W) and east (E).

distinct zones in the wetland that may compartmentalize denitrification capacity (Suchy et al., 2019). The effect of vegetation cover type on DNRA has been scarcely explored in wetland ecosystems (Chen et al., 2021; Hoffman et al., 2019; Zhang et al., 2017).

The objective of our research was to evaluate (a) what proportion of NO_3^- attenuation occurs through denitrification and DNRA in the Salt River wetlands, (b) how vegetation cover and type (*L. peploides*, *Typha spp*, and non-vegetated) affect carbon availability, and (c) how patch type and carbon availability affect denitrification, DNRA, and the DNRA to denitrification ratio (DNRA:denitrification). We hypothesized that (a) wetland patches with vegetation cover would have higher organic carbon than unvegetated patches, and patches of *L. peploides* would have higher organic carbon than *Typha spp* due to structural differences, (b) vegetated patches with higher organic carbon availability would have higher denitrification and DNRA rates due to higher carbon availability, and (c) DNRA:denitrification would be higher in patches with higher carbon availability.

2. Materials and Methods

2.1. Site Information

The Salt River in Phoenix, Arizona, USA, is a tributary of the Gila River, and together the two rivers form the main desert portion of the larger Lower Colorado River Basin. The Salt River has been heavily modified by dams and diversion canals to support agricultural and municipal water demand (Fitzhugh & Richter, 2004; Larson et al., 2005). All flow is diverted into canals upstream of Phoenix and, as a result, the stretch of river in the city lacks any direct water supply from the upstream watershed. The urban river channel now serves as a recipient system for water from treated municipal effluent, irrigation runoff, and stormwater runoff (Banville & Bateman, 2012; Bateman et al., 2015). Some drains provide a near-perennial water source to the channel while others are more episodic in water supply (Suchy et al., 2019). There are four identified perennial accidental wetlands in the Salt River in the Phoenix Metro area (Bateman et al., 2015; Suchy et al., 2019).

Sampling sites were located within the Central Arizona-Phoenix Long Term Ecological Research study area (CAP-LTER) along a 2-km reach of the Salt River channel where urban accidental wetlands have formed due to discharges of urban baseflow from a series of storm drains. These drains discharge enough baseflow for the study wetlands to remain inundated for more than 85% of the year (Suchy et al., 2019). The source of the urban baseflow is largely unknown, but does not include municipal wastewater, which is transported through a separate pipe system. Rather, various human activities in the watershed such as flood irrigation of lawns, car washing, or pool maintenance are the likely source of the baseflow. The sampling sites were located near the 7th Avenue (7A) and Central Avenue (CEN) bridges over the river channel (Figure 1).

Water depth in the wetlands fluctuates depending on the quantity of base- or stormflow at a given time; however, point estimates of depth during baseflow range from 2 cm near wetland edges where vegetation is dense to near 100 cm in wetland centers where no vegetation is present. We sampled in three dominant patch types: patches without vegetation (hereafter "open"), patches dominated by *Ludwigia peploides* (LUPE) and patches dominated by *Typha* spp. (TYSP). *Typha* spp patches were either *Typha domingensis*, *Typha latifolia*, or a mix of both. These species were indistinguishable in the field and were assumed to be functionally similar for the purposes of the study. Open, LUPE, and TYSP patches account for roughly 39%, 30% and 17% of wetland area, respectively, with other vegetation accounting for the remaining 14% of cover (see Bateman et al., 2015 supplementary info for a list of taxa).

2.2. In-Situ Push-Pull Incubation

We conducted an *in-situ* push-pull experiment (modified from Addy et al., 2002) with isotopically labeled NO_3^- to measure denitrification and DNRA. The push-pull method involves enriching field-collected water with the

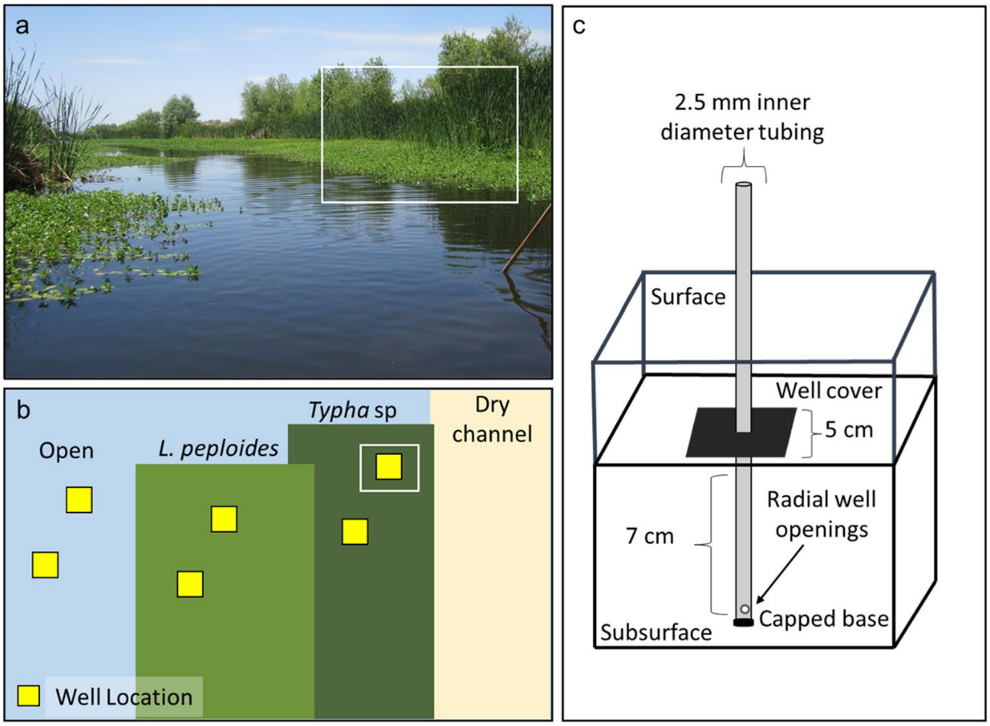

Figure 2. A picture of the 7th Avenue wetland site showing the three focal patch types: *Typha spp*. in the background and *Ludwigia peploides* and unvegetated open patches in the foreground (a). The white box is schematically represented in (b), showing how wells are arranged within patches at a sampling location; (c) shows a schematic diagram of the well sampling design.

biologically reactive tracer (NO_3^- in this case) and an unreactive tracer to account for dilution, injecting the water into the subsurface ("push"), and sampling from the plume after an incubation period ("pull"). We conducted tests over four dates in June 2016 with experiments conducted in two wetland sites (7A and CEN). At each site, we identified two patches belonging to each of the three dominant cover types (open, TYSP, LUPE) for a total of four patches of each dominant cover type. In each patch, we placed two wells for a total of eight push-pull tests per patch cover type (24 tests total; Figure 2). We used 2.5-mm inner-diameter wells inserted to a depth of 7 cm with radial perforations around the bottom 1 cm and capped at the base. Each well had 2–20 cm of overlying surface water, and wells within the same patch were at least 1.5 m apart. We placed a 5-cm square rubber cap that was flush with the soil surface on each well to prevent drawdown of surface water along the well sides during sample collection (Figure 2). Two wells, one well in a LUPE patch in CEN and one well in a TYSP patch in 7A, became dislodged from the soil during the incubation, preventing collecting final samples. As a result, there were 22 total push-pull tests analyzed.

We collected initial background porewater gas samples by attaching a 60 mL syringe to the well with a two-way stopcock. We purged the first 10 mL of water from the well prior to sample collection in order to ensure we were collecting water that had been mixed with the soil surrounding the well. We slowly withdrew the purge water from the well, the stopcock was locked, the syringe detached, and the 10 mL discarded. Next, 30 mL of porewater was withdrawn for collection of a dissolved dinitrogen gas (N_2) sample for analysis of the concentration of the N_2 gas species including $^{29}N_2$ and $^{30}N_2$. The sample was transferred to a 12-mL Exetainer (Labco Lampeter) by filling from the bottom up, overfilling approximately twice before poisoning with 20 μL saturated zinc chloride ($ZnCl_2$) solution to prevent further microbial activity and then capping. Dissolved gas samples in Exetainers were stored upside down in 1 L bottles filled with field water. We then collected an additional 340 mL of porewater, to which we added a 20 mL dosing solution that raised the concentration of NO_3^- by 7 mg N L^{-1} at 20 at% ^{15}N (from $NaNO_3^-$ and 99 at% ^{15}N-KNO_3^-) and 20 mg L^{-1} bromide (Br^-, added as KBr). We chose the 7 mg N L^{-1} NO_3^- amendment level to be similar to stormflow NO_3^- conditions in the wetlands (Palta et al., 2017). Previous sampling revealed that background NO_3^- concentration in the porewater was below or near the instrument detection limit of 5 μg N L^{-1} and we therefore assumed background NO_3^- was negligible. Care was taken to minimize introduction of bubbles into the solution. We then subsampled 170 mL of the dosed water and filtered initial aqueous samples using 0.45 μM mixed cellulose ester syringe filters (Fisher Scientific, Hampton, NH, USA), and stored the samples on ice for later analysis of NO_3^- and NH_4^+, $^{15}NH_4^+$, Br^-, and dissolved organic carbon (DOC). The remaining 190 mL of tracer-enriched solution was injected ("pushed") into the well. The Br^- was added as a hydrologic tracer that is expected to be biologically inert; thus, changes in Br^- concentration will reflect dilution of the dosing solution when added to the well. After a 30-min incubation from the time that the sample was pushed, we collected ("pulled") samples. The short incubation period was chosen based on pre-tests demonstrating that a 30-min incubation period was sufficiently long to observe change in the NO_3^- and NH_4^+ concentration while still recovering approximately 20% of the added Br^- tracer. While this level of recovery is low, it is similar to that reported in other studies (e.g., Aoki & McGlathery, 2017). In the pulled sample, we first collected the dissolved N_2 sample (as above) followed by additional samples for analysis of NO_3^-, NH_4^+, $^{15}NH_4^+$, and Br^- (we assumed DOC concentration would not change substantially over a 30-min period). All samples were stored on ice until returned to the lab. Sample vials for NO_3^-, NH_4^+, Br^-, and DOC were stored at −30°C for 4–12 weeks until analysis. Samples for $^{15}N\text{-}NH_4^+$ were immediately processed upon return from the field.

2.3. Chemical Analyses

We determined N_2 gas concentration and isotopic composition using a membrane inlet mass spectrometer (MIMS; Bay Instruments; An et al., 2001; Kana et al., 1994) outfitted with a furnace heated to 600°C to minimize interference from NO^+ production (Lunstrum & Aoki, 2016). We ran air-equilibrated standards every 5–8 samples. Both samples and standards were run at temperatures within 2°C of the field collection temperature. The instrument provides the absolute masses of $^{29}N_2$ and $^{30}N_2$ isotopes. These were converted to excess concentration of $^{29}N_2$ and $^{30}N_2$ relative to air-equilibrated water. Two sample vials broke during transport, resulting in insufficient data to calculate change in N_2 for one LUPE sample in 7A and one TYDO sample in CEN.

We measured $^{15}N\text{-}NH_4^+$ by headspace diffusion of filtered water samples (Holmes et al., 1998). Excess sodium chloride (NaCl), magnesium oxide (MgO), and an encapsulated acidified filter was added to each sample, capped, and placed on a shaker table for 2 weeks at 145 rpm. After shaking, we removed, dried, and encapsulated filters in tins for isotopic analysis. All $^{15}N\text{-}NH_4^+$ samples were analyzed by an Elementar Vario EL Cube or Micro Cube elemental analyzer (Elementar Analysensysteme GmbH) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd.) at the Stable Isotope Laboratory of the University of California, Davis. Nitrate and NH_4^+ concentrations were determined with a Lachat QC8000 flow-injection analyzer (Lachat Instruments). Bromide concentration was determined with a Dionex ICS2000 ion chromatograph (Dionex Corporation). Dissolved organic carbon concentration was determined with a Shimadzu TOC-VC/TN (Shimadzu Corporation). Any ion or carbon concentration below the range of the instrument standard curve was assigned a value of one-half of the lowest concentration on the instrument standard curve.

2.4. Soil Properties

To determine soil physical properties of each patch, we collected saturated soil cores of known volume from the same locations used for the push-pull experiment or the nearest saturated soil to the experiment location on 15 June 2017. We assumed soil properties would not change substantially in the year since the experiment. We recorded the saturated core mass, then dried the cores at 60°C to constant mass and reweighed. We assumed a 1 g per 1 mL mass-volume relationship for the water mass lost to calculate the porosity of the soil. Soil core data are available in Table S1 in Supporting Information S1.

2.5. Denitrification and DNRA Calculations

To evaluate the proportion of NO_3^- consumed through denitrification and DNRA (Objective 1), we performed a mass-balance analysis of added ^{15}N recovered in the N_2 and NH_4^+ pools. We calculated the dilution-corrected mass of ^{15}N in $^{29}N_2$, $^{30}N_2$, and $^{15}N\text{-}NH_4^+$ in final samples based in the change in the Br^- concentration. The mass of ^{15}N recovered through denitrification and DNRA was subtracted from the added ^{15}N mass to estimate the unaccounted for ^{15}N that either remains unconsumed in the NO_3^- pool or was consumed through other processes. The masses were normalized to a 30-min incubation period to account for small differences in the incubation periods for individual wells. We present results as percent and mass ^{15}N recovered by patch type and across all samples.

To calculate denitrification of the added NO_3^-, we dilution-corrected final samples of $^{29}N_2$ and $^{30}N_2$ based on the change in Br^- concentration between initial and final samples. We calculated the direct denitrification rate as the change in ^{15}N-N_2 concentration from the added ^{15}N-NO_3^-. First, we calculated the ^{15}N-N_2 production rate based on the excess $^{29}N_2$ and $^{30}N_2$ signals in the N_2 pool (Nielsen, 1991):

$$D_{15} = \ 2p_{30} + p_{29}$$

where p_{30} and p_{29} are the net production rate of $^{30}N_2$ and $^{29}N_2$, respectively. We then divided D_{15} by the proportion of N added as ^{15}N-labeled NO_3^- (0.2) to get the direct denitrification rate ("denitrification", hereafter). We do not include coupled nitrification-denitrification in the denitrification estimate due to uncertainties associated with the low level of tracer. DNRA was calculated as the net production rate of ^{15}N-NH_4^+ (Koop-Jakobsen & Giblin, 2010) divided by the proportion of N added as ^{15}N-labeled NO_3^-. This calculation captures the DNRA rate of the added NO_3^- but does not include DNRA from NO_3^- produced through nitrification over the course of the incubation period. The denitrification and DNRA rate were normalized to mass of dry wetland soil per hour. Since the denitrification and DNRA rates are based on production from the added NO_3^- that was targeted to simulate stormwater NO_3^- concentration, the rates should be interpreted as representative of stormflow NO_3^--supply conditions.

2.6. Statistical Analysis

To evaluate the effect of patch cover type on DOC concentration (Objective 2), we performed a two-way analysis of variance (ANOVA) including cover type and site as independent variables. We included site in the model as the two study wetlands were located near outfalls of two different storm drains, which may have affected initial water quality. We also tested for a potential interaction among cover type and site. If the interaction between cover type and site was not significant it was not included in the final model. In the process of collating the data, we found variation in the starting NO_3^- concentration in the wells following the addition of the dosing solution, although the overall concentration remained high (3–7 mg N L^{-1}). We therefore included the starting NO_3^- concentration as an independent variable in the final model to account for this variability. Tukey's HSD post hoc tests were used to further determine pairwise significance levels when necessary.

To evaluate the effect of patch cover type and DOC concentration on denitrification rate, DNRA rate, and DNRA:denitrification (Objective 3), we performed multiple linear regressions. We included a site factor and the starting NO_3^- concentration in model development in case these factors remained important. In addition, we tested the NO_3^- to DOC ratio (NO_3^-:DOC) as an explanatory variable. We built initial models for each rate by including one explanatory variable. If an explanatory variable was significantly related to a rate, a second set of models was constructed to test if the addition of a second explanatory variable would increase the model fit. We compared models for each rate using Akaike's Information Criterion (AIC) to ensure that we selected models that accounted for the most variation in the response variable while maintaining parsimony. A model that is lower in AIC by at least two is commonly used to denote a model that explains more variation without overly increasing model complexity (Burnham & Anderson, 2004). We log-transformed DOC concentration and DNRA rate to adhere to assumptions of normality and equality of variance. Since our response variables include both normal and log-normal distributions, we report summary statistics as means and 95% confidence intervals. Continuous explanatory variables (NO_3^-, DOC, NO_3^-:DOC) were centered by transforming to z-scores for inclusion in regression models. The patch variable was included in models as a dummy code with open patches as the base group. If the patch variable was included in the final model, we switched the base group to the LUPE patch in order to check for all pair-wise comparisons among patches. We assessed the residual variation for normality in all models. All analyses were conducted in R (R Core Team 2021).

Table 1
Mass Balance for Push-Pull Experiments in Salt River Accidental Wetlands

Patch	DNRA	Denitrification	Unaccounted ^{15}N
Units	%	%	%
OPEN	2.6 (1.5–3.6)	14.5 (6.6–22.4)	82.9 (74.3–91.6)
LUPE	4.5 (0.2–8.7)	21.8 (6.4–37.2)	73.7 (59.1–88.3)
TYSP	0.9 (0.4–1.4)	17.1 (3.7–30.5)	82.0 (68.5–95.4)
All Patches	2.7 (1.4–3.9)	17.5 (11.9–23.1)	79.9 (74.1–85.6)
Units	mg ^{15}N	mg ^{15}N	mg ^{15}N
OPEN	0.03 (0.01–0.04)	0.15 (0.06–0.23)	0.83 (0.73–0.94)
LUPE	0.05 (0.01–0.09)	0.24 (0.07–0.40)	0.80 (0.64–0.96)
TYSP	0.01 (0.00–0.02)	0.18 (0.04–0.31)	0.86 (0.71–1.01)
All Patches	0.03 (0.02–0.04)	0.18 (0.12–0.24)	0.83 (0.77–0.89)

Note. Values are mean (95% confidence intervals in parentheses) percent mass or total mass of ^{15}N recovered at the conclusion of the incubation through denitrification, DNRA, and—by mass balance—the amount unaccounted for NO_3^- that either remains unconsumed or was consumed by other processes ("Unaccounted ^{15}N"). Means are for each patch type: unvegetated patches (OPEN), *Ludwigia peploides* (LUPE), and *Typha spp*. (TYSP) and across all patch types ("all patches").

3. Results

3.1. Objective 1: Proportion of NO_3^- Attenuated Via Denitrification and DNRA in the Salt River Wetlands

Denitrification consumed a higher proportion of the added ^{15}N-NO_3^- (mean, 95% confidence interval (CI): 17.5%, 11.9%–23.1%) than DNRA (2.7%, 1.4%–3.9%; Table 1). By mass balance, a majority of the added ^{15}N-NO_3^- was either unconsumed or consumed through other unmeasured processes (79.9%, 74.1%–85.6%).

3.2. Objective 2: Effect of Wetland Cover Type and Site on and DOC and NO_3^- Concentration

We found DOC and initial NO_3^- concentrations were similar among patch types but differed between the two wetland sites (Figure 3). DOC concentration was significantly higher ($F_{[1,20]} = 15.20$, $p < 0.001$) at the 7A site (mean, 95% CI: 12.29, 9.75–15.49 mg/L) compared to the CEN site (8.03, 7.45–8.65 mg/L). Similarly, the initial NO_3^- concentration was significantly higher ($F_{[1,20]} = 7.26$, $p = 0.014$) at the 7A site (5.16, 4.62–5.69 mg N/L) compared to the CEN site (4.31, 3.86–4.76 mg N/L).

3.3. Objective 3: Effect of Patch Cover and Initial Conditions on Nitrogen Rates

In final regression models we found that patch cover significantly affected denitrification (final model: $F_{[2,17]} = 4.89$, $p = 0.021$, $R^2 = 0.29$) and DNRA rates ($F_{[3,18]} = 8.87$, $p < 0.001$, $R^2 = 0.53$; Table 2, Figure 4). Specifically, we found that the LUPE patches had significantly higher denitrification (4.35, 1.31–7.39 μg N g dry soil^{-1} hr^{-1}) and DNRA rates (0.58, 0.2–1.66 μg N g dry soil^{-1} hr^{-1}) compared to the open patches (0.19, 0.12–0.31 μg N g dry soil^{-1} hr^{-1} and 1.24, 0.54–1.94 μg N g dry soil^{-1} hr^{-1}, respectively; Figure 4). In addition, the TYSP patches exhibited significantly lower DNRA rates (0.22, 0.13–0.32 μg N g dry soil^{-1} hr^{-1}) than the LUPE patches. We also found that the DOC concentration was significantly negatively correlated with DNRA rates (Table 2, Figure 5). DNRA:denitrification was significantly negatively correlated with the starting NO_3^- concentration ($F_{[1,18]} = 5.39$, $p = 0.032$, $R^2 = 0.19$; Table 2, Figure 6). An alternative model of DNRA:denitrification based on the site variable had an AIC (−6.7, Table S2 in Supporting Information S1) similar to the model with the initial NO_3^- concentration (−7.6) but explained less variation (R^2 of 0.15 vs. 0.19). In this alternative model, DNRA:denitrification was higher at the CEN site (0.30, 0.14–0.46) than the 7A site (0.12, 0.02–0.22).

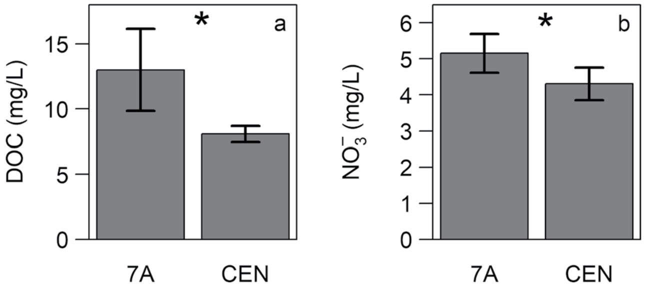

Figure 3. Mean initial dissolved organic carbon (DOC); (a) and nitrate (NO_3^-; (b) concentration at 7th Avenue (7A) and Central Avenue (CEN) sites. Bars represent 95% confidence interval of the mean. Asterisks indicate significant difference among group means based on a one-way analysis of variance (ANOVA) for DOC ($F_{[1,20]} = 15.20$, $p < 0.001$) and NO_3^- ($F_{[1,20]} = 7.26$, $p = 0.014$).

4. Discussion

Wetlands are important hotspots of nitrogen removal in urban environments that suffer from nitrogen pollution. Research to date has focused on understanding nitrogen removal through denitrification; however, DNRA may compete with denitrification for NO_3^- while conserving nitrogen through transformation to NH_4^+. Our findings add DNRA to the nutrient-attenuating capacity of the Salt River accidental wetlands identified in previous studies (Palta et al., 2016, 2017; Suchy et al., 2019), and confirm that denitrification is a substantial portion of this capacity. We also found that lower NO_3^- concentration was associated with a higher DNRA:denitrification, suggesting the potential for a shift toward the process that retains nitrogen (i.e., DNRA) when NO_3^- availability is limited. Finally, our findings illuminate how vegetation species can differently affect the magnitude of DNRA, a rarely studied effect on patterns of DNRA in freshwater systems (Zhang et al., 2017).

Table 2
Final Multiple Regression Models for Flux Rates Measured by Push-Pull Method

Dependent variable	N	LUPE	TYSP	NO_3^-	DOC	R^2
DNRA[a]	22	1.27 (0.38)**	−0.61 (0.37)	-	−0.47 (0.16)**	0.53***
Denitrification	20	1.31 (0.40)**	0.61 (0.40)	-	-	0.32*
DNRA:Denitrification	20	-	-	−0.09 (0.04)*	-	0.19*

Note. The number of observations in each model and potential variables included in each model are patche type—a dummy coded variable with unvegetated patches (OPEN) as the base group and *Ludwigia peploides* (LUPE) and *Typha spp*. (TYSP) patches as the comparison groups—the initial NO_3^- concentration (NO_3^-) and the initial dissolved organic carbon concentration (DOC). Values are coefficient estimates (standard error in parentheses). A dash (−) indicates the variable was not included in the final model. The adjusted multiple R^2 (R^2) value for the final model shows the variation explained. Asterisks indicate significance level: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

[a] DNRA rate was natural log transformed.

4.1. Denitrification and DNRA Contribute Significantly to NO_3^- Attenuation in Salt River Accidental Wetlands

We found DNRA could account for as much as 40% of NO_3^- reduction (DNRA plus denitrification rate), but was lower than denitrification in all wells, accounting for an average of 15% of NO_3^- reduction of the added tracer across wells. Our estimate of overall allocation of the added $^{15}N\text{-}NO_3^-$ in the experiment was 17% to denitrification, 3% to DNRA, and 80% unaccounted for NO_3^-. The NO_3^- not consumed through denitrification or DNRA may have been consumed through other unmeasured processes or remain unconsumed in the NO_3^- pool. Assuming the NO_3^- pool at the conclusion of the incubation has the same isotopic composition as the start, the mean proportion of unconsumed NO_3^- was 49% and the amount of $^{15}N\text{-}NO_3^-$ consumed though unmeasured processes was 31%. This conservative estimate would mean other consumption processes were larger than the proportion consumed through denitrification and DNRA combined. Other studies of mass balance of added NO_3^- to wetlands have found similar proportions assimilated by plants suggesting plant assimilation may be the dominant mechanism of removal in vegetated patches (Matheson et al., 2002; Messer et al., 2017; Nijburg & Laanbroek, 1997; Rückauf et al., 2004). Additionally, our experiment took place during June, near the peak of the growing season for the wetlands, when plants compete with microbial consumers of NO_3^- (Groffman et al., 1992; Hall et al., 2009; Pinay et al., 1993), and thus can account for the majority of NO_3^- consumption (Mulholland et al., 2009). Interestingly, open patches with no vegetation cover also had similar proportions of unaccounted for ^{15}N as the vegetated patches, which implies a N removal mechanism other than plant uptake. These open patches often had extensive biofilms present that may include microbial and algal communities with a high capacity for assimilative NO_3^- uptake (Larson & Greenway, 2004). It is important to note that soil adsorption of NO_3^- or NO_3^- converted to NH_4^+ (as NH_4^+ is less mobile in soils than NO_3^-) could also contribute to the pool of unrecovered NO_3^-. Matheson et al. (2002) found that immobilization of added NO_3^- in soil was similar in planted and unplanted wetland soil microcosms and accounted for roughly double the NO_3^- uptake from plants. Additional experiments are required to estimate the adsorption rate for NO_3^- and NH_4^+ (Gardner et al., 1991).

The DNRA rate in this study was 1–2 orders of magnitude higher than that measured in other freshwater wetland ecosystems (Rahman, Grace, et al., 2019; Rahman, Roberts, Grace, et al., 2019; Scott et al., 2008; Wang et al., 2020), stream sediments (Cheng et al., 2016; Hoellein et al., 2017; Storey et al., 2004; Washbourne et al., 2011), and lake sediments (Nogaro & Burgin, 2014). In addition, DNRA rate in this urban wetland was substantially higher than reported for coastal (Bernard et al., 2015; Giblin et al., 2013; Hoellein et al., 2015) and terrestrial ecosystems (Rütting et al., 2011). One possible explanation for the higher rate is that the level of NO_3^- addition used in the present study was high relative to other studies in aquatic ecosystems and may have stimulated higher DNRA rates. We chose to use a high NO_3^- amendment to mimic the concentration of NO_3^- the study wetlands experience during storm events (Palta et al., 2017). The range of DNRA rates in this study overlapped with the range reported in systems that receive high nutrient inputs and used similar levels of NO_3^- amendment for determining DNRA rate, including the groundwater of a constructed wastewater treatment wetland (Jahangir et al., 2017), eutrophic lake margin sediment with emergent vegetation (Nijburg & Laanbroek, 1997), and lakes impacted by historic mining and carbon loading (Nizzoli et al., 2010). Even though DNRA rate did not vary with NO_3^- concentration within sites in this study, the variation in DNRA among disparate ecosystems exhibiting a

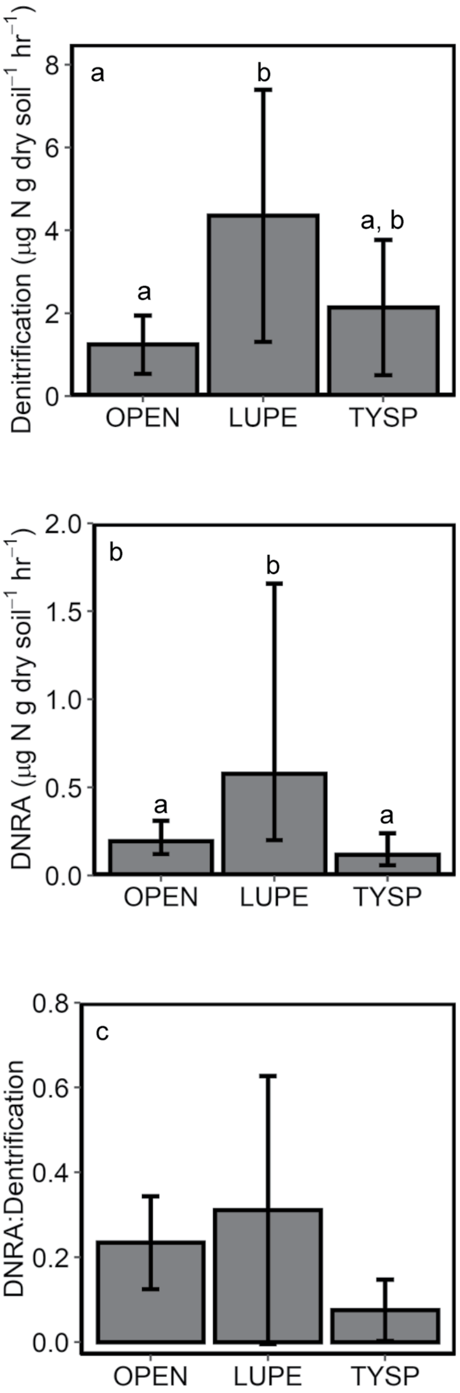

Figure 4. Mean and 95% confidence interval for denitrification rate (a), DNRA rate (b), and DNRA:denitrification ratio (c) by patch type: unvegetated (OPEN), *L. peploides* (LUPE), and *Typha spp*. (TYSP). Letters above bars denote groups with statistically significant differences.uploaded separately. Each figure should be one complete, cohesive file (please do not upload sub-figures or figure parts in separate files).

broad range of NO_3^- concentration suggests that DNRA may be sensitive to ecosystem NO_3^- status.

Notably, Suchy et al. (2019) reported potential denitrification rates (denitrification under optimal low oxygen, high carbon and NO_3^- conditions) of a similar magnitude to our findings for the same sites. Because measurement of potential denitrification reflects a maximum possible rate under ideal conditions, the similarity of denitrification rates suggests that these accidental wetlands have a high capacity to attenuate NO_3^- with few limitations when NO_3^- is present.

The NO_3^- removal capacity of the Salt River wetlands has potentially important implications for the Phoenix metropolitan area's broader nitrogen budget (Baker et al., 2001). The perennial wetlands in this study are part of a matrix or wetlands along a 30 km stretch of the Salt River that receive water mostly from drains that deliver runoff from the urban landscape that is enriched in NO_3^-. While these wetlands occupy a small portion of the overall landscape, they do receive the bulk of the drainage during storms and thus would be important locations of nutrient removal. Previous work has demonstrated that these wetlands have a high capacity for NO_3^- removal (Palta et al., 2016) and high potential for denitrification (Suchy et al., 2019). Our study adds that both denitrification and DNRA contribute to NO_3^- removal in these wetlands, resulting in both loss of nitrogen via denitrification and decreased mobility of nitrogen as NH_4^+ produced from DNRA. Future water conservation strategies for the area may result in a decrease in water supply to the Salt River channel and shift these wetlands from perennial to ephemeral. A reduction in water supply will likely reduce the denitrification capacity (Suchy et al., 2019) as well as the DNRA rate. Such an outcome may shift the location of NO_3^- retention in the urban landscape or result in increased export of NO_3^- to the groundwater.

Several factors may have contributed to an underestimate of denitrification and DNRA. First, our tracer technique only allows determination of denitrification of the added tracer and does not include coupled nitrification-denitrification or adjustments based on nitrogen fixation (An et al., 2001; Nielsen, 1992). We can infer the presence of coupled nitrification-denitrification in these wetland sites because the NO_3^- concentration increased over the incubation period in 4 of 22 wells. This combined with the positive denitrification and DNRA rates that deplete the NO_3^- pool indicates the presence of nitrification and likely coupled nitrification-denitrification. The presence of nitrification may have also depleted the NH_4^+ produced through DNRA over the incubation period, reducing the estimated DNRA in these sites. The removal of N_2 through nitrogen fixation could lead to a further underestimate of denitrification. The observed emergence of bubbles and sulfureous odor when sediments were disturbed may indicate the wetlands contain sulfide that can inhibit complete denitrification and produce N_2O through incomplete denitrification. Second, we may have lost N_2 through degassing to the surface or air-filled pore spaces and gas exchange with roots and rhizomes (Koop-Jakobsen & Giblin, 2009). These loss pathways would result in disproportionate loss of gas relative to the aqueous Br^- conservative tracer used in this experiment, resulting in an underestimate of denitrification (Koop-Jakobsen & Giblin, 2009). Finally, we may have underestimated DNRA due to NH_4^+ adsorption to soil particles, assimilation into plant and microbial biomass, or via nitrification. The organic-rich nature of the wetland soils could indicate that the rate of adsorption to soil particles is considerable in these systems (Vymazal, 2007). In addition, the measurements were

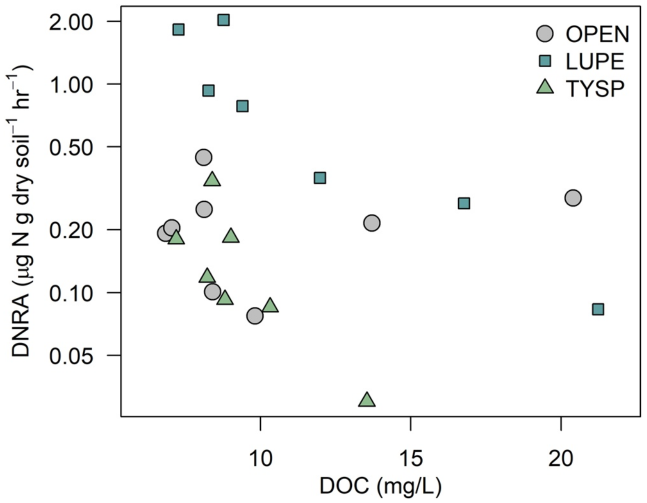

Figure 5. DNRA rate plotted against dissolved organic carbon (DOC) concentration within unvegetated (OPEN, circles), L. peploides (LUPE, squares), and Typha spp. (TYSP, triangles) patches. Note that the DNRA rate is log-transformed.

collected near the height of peak biomass, a time when plant uptake of nutrients will be maximal. However, given the short incubation period (30 min), we expect that remineralization of assimilated NH_4^+ or NO_3^- to be minimal during the experiment.

4.2. DNRA Unrelated to NO_3^- and Negatively Correlated With DOC

Our findings are consistent with other studies that found that DNRA was unrelated to NO_3^- concentration (Koop-Jakobsen & Giblin, 2010; Nizzoli et al., 2010; Nogaro & Burgin, 2014; Sotta et al., 2008). We did find a weak negative correlation between DNRA:denitrification and the starting NO_3^- concentration. A common hypothesis posits that DNRA will be favored over denitrification in conditions with limited electron acceptors or a high organic carbon to NO_3^- ratio because DNRA consumes a higher number of electrons per unit NO_3^- than denitrification (Burgin & Hamilton, 2007; Tiedje, 1988). Several studies have found support for this hypothesis in freshwater wetlands (Matheson et al., 2002; Scott et al., 2008), streams (Crenshaw et al., 2010; Storey et al., 2004), salt marshes (King & Nedwell, 1985), and agricultural soils (Fazzolari et al., 1990). However, Matheson et al. (2002) argued that the relationship between high organic carbon to NO_3^- ratio and DNRA is one where an increase in carbon increases oxygen demand, thereby creating more strongly reducing conditions that are more favorable for DNRA than denitrification. We may have observed this, based on our finding that DNRA was consistently highest in the LUPE patches where conditions may have been more strongly reducing compared to the TYSP or open patches, owing to a combination of higher carbon quality and lower oxygen delivery via root systems.

Our finding that DOC concentration was negatively correlated with the DNRA rate was surprising. However, because the DOC concentration differed between the two sites, the DOC could be correlated with another site-specific difference such as soil structure or inundation frequency, both of which can affect denitrification as well as presumably DNRA (Suchy et al., 2019). The difference in DOC concentration between sites may indicate that the source catchments have different characteristics or activities that have consequences for water chemistry (Walsh et al., 2005). Newcomer et al. (2012) found that urban streams differed in DOC quantity and composition based on the source types within the drainage. These differences in catchments may be driving differences in water chemistry between the sites and consequently DNRA.

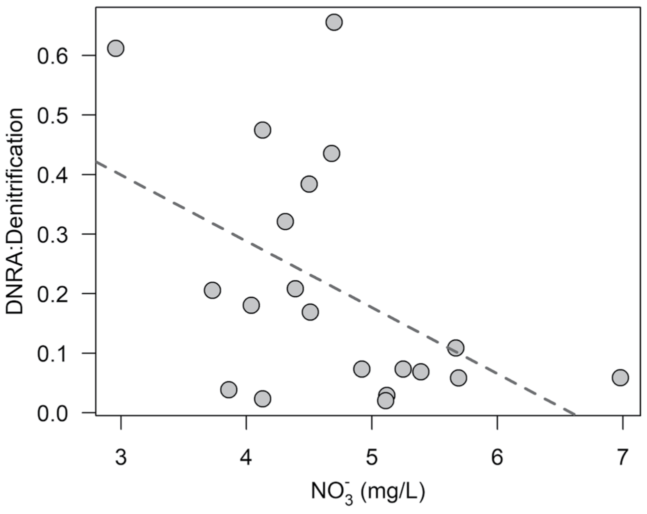

Figure 6. DNRA:denitrification as a function of starting NO_3^- concentration. Dashed line shows the regression relationship ($F_{[1,18]} = 5.39$, $p = 0.032$, $R^2 = 0.19$).

Previous studies have generally found either no relationship or a positive correlation between DNRA and measures of carbon, including total organic matter, extractable soil carbon, total organic carbon, and DOC in freshwater ecosystems (Cheng et al., 2016; Li et al., 2019; Nizzoli et al., 2010; Shan et al., 2016; Wang et al., 2020). The DOC concentration provides a metric for quantity of available carbon, but little information about the quality of the available carbon. DOC in freshwater ecosystems is composed of humic substances, fulvic acids, low-molecular-weight carbohydrates, carboxylic acids, and amino acids (Findlay & Sinsabaugh, 2003; Reitsema et al., 2018). However, the proportion of each component of DOC can vary widely. It is possible that the high DOC in our wetland study sites may be dominated by high molecular weight and humic substances that are not readily bioavailable to heterotrophic NO_3^- reducing organisms; thus, higher DOC concentration is not necessarily associated with higher organic carbon availability for heterotrophic processes.

The association between DNRA and organic carbon may also depend on the type of DNRA process taking place. While fermentative DNRA requires a carbon source and is thought to be more common in freshwater systems (Burgin & Hamilton, 2007), there is evidence that sulfur-mediated DNRA is present in freshwater systems as well (Brunet & Garcia-Gil, 1996; Rahman et al., 2019). Sulfur-mediated DNRA is not dependent on carbon availability. We noted gas bubbles released and sulfurous odor when some wetland soils were disturbed, indicating potential presence of hydrogen sulfide that could be a substrate for sulfur-mediated DNRA. Further research is needed to establish which form of DNRA is occurring in the Salt River wetlands.

4.3. Vegetation Cover Type Affects DNRA Rate and Denitrification Rate Differently

Our study indicates that vegetation patch cover type differently affects denitrification and DNRA in the Salt River wetlands. The LUPE patches had significantly higher rates compared to the open patches for both denitrification and DNRA, and were also higher than TYSP patches with respect to DNRA rate. The TYSP patches had higher mean rates than open patches for denitrification, but the high variability lead to statistical overlap between the two groups. Several prior studies have found that the presence of plants increases denitrification rate, but it is less clear if plant species has an effect (Alldred & Baines, 2016; Groffman et al., 1996; Hume et al., 2002; Zhang et al., 2017). Plant patches can enhance NO_3^- reduction by acting as a source of organic carbon to soil through litter production (Gift et al., 2010; McClaugherty et al., 1982) and root exudation or decomposition (Schade et al., 2001). We found patches were similar in carbon quantity with respect to DOC concentration, contrasting with Suchy et al. (2019) who found that organic matter differed among patch types in the Salt River wetlands. Nevertheless, denitrification was not limited by carbon in either vegetated or unvegetated patches in either study. However, as stated in the previous section, there may be differences in plant patches with respect to carbon quality. The composition of litter with respect to structural versus more labile forms of carbon can affect the supply of microbially available forms of carbon (Manzoni et al., 2008). A preliminary study in the Salt River wetlands found that LUPE has a lower tissue C/N ratio compared to TYSP suggesting LUPE has more available labile carbon than TYSP (Cornwell et al., 2008; Hume et al., 2002). It is possible that higher carbon quality derived from LUPE litter may be driving higher denitrification and DNRA rates in these patches, but this hypothesis warrants further investigation.

Another potential explanation for the lower DNRA in TYSP patches compared to LUPE patches may be related to aeration of the subsurface via roots that alter redox conditions. For example, *Typha latifolia*, which made up some of the TYSP patches, can inhibit methanogenesis, an obligate anaerobic process, in soil by supplying oxygen through roots (Jespersen et al., 1998). In contrast, *Ludwigia* species found in the LUPE patches are floating aquatic macrophytes and while they can aerate with their upwards growing roots (Ellmore, 1981), the overall effect of dense *Ludwigia* mats such as those seen in the Salt River wetlands is an accumulation of silt and reduction in water column oxygen (Gérard et al., 2014). Both denitrification and DNRA require low-oxygen conditions, but denitrifying taxa are commonly facultative anaerobes whereas microorganisms that carry out DNRA are more often obligate anaerobes. It may therefore be the case that denitrification can occur at high levels in either plant patch, tolerating both anoxic and sub-oxic conditions, whereas DNRA is restricted to the LUPE patches that are more consistently anoxic. Nijburg and Laanbroek (1997) similarly reported that DNRA was higher in decomposing stands of *Phragmites australis* compared to healthy stands due to lower oxygen availability. On the other hand, some studies have found that denitrification is more sensitive to oxygen while DNRA is more sensitive to carbon to nitrogen ratios, both of which can be controlled by overlying vegetation (Fazzolari et al., 1998; Washbourne et al., 2011).

5. Conclusions

Wetland ecosystems, especially in urban contexts, are touted for their nutrient attenuating capacity. While denitrification has been a central focus in the context of reducing NO_3^-, DNRA requires similar conditions and can account for a substantial proportion of NO_3^- consumption. We found that DNRA across patches in the Salt River accidental wetlands accounted for as much as 40% of combined denitrification and DNRA. Understanding the factors that mediate the ratio of DNRA to denitrification is critical for predicting nitrogen retention versus loss in this ecosystem. Whereas in denitrification nitrogen is lost to the atmosphere, a preponderance of DNRA means that nitrogen is retained within the ecosystem in the less-mobile NH_4^+ form, which is available for uptake and further transformation. The relative importance of denitrification and DNRA over different seasons may change as well. For example, Suchy et al. (2019) found that the patch type with the highest potential denitrification rate varied by season. Similar to this study, LUPE had the highest potential denitrification in the summer, but other wetland patches had higher rates in the winter months (Suchy et al., 2019). The LUPE patches had the highest

DNRA rates in the present study but perhaps under different seasonal conditions, other patches become important sites of NO_3^- reduction. Further research is needed to establish the ultimate fate of the NH_4^+ produced from DNRA and seasonal differences in the Salt River wetlands.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

All data generated from this study and the code used to conduct the analysis can be accessed through the Environmental Data Initiative repository at https://doi.org/10.6073/pasta/955ff0ecc46a0be0a3d251a6e02af908.

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